Behavioral Ecology, 1999, v.10, n.5, pp.572-577.
Online ISSN: 1465-7279
Print ISSN: 1045-2249
DOI:10.1093/beheco/10.5.572
http://www.oxfordjournals.org/
http://beheco.oxfordjournals.org/
This is a pre-copy-editing, author-produced PDF of an article accepted for publication in Behavioral Ecology *following peer review. The definitive publisher-authenticated version* Behavioral Ecology Vol. 10 No. 5: 572-577 *is available online at:* http://beheco.oxfordjournals.org/cgi/reprint/10/5/572

A dynamic model of group-size choice in the coral reef fish *Dascyllus albisella*

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We developed a dynamic programming model of group size choice for settling coral reef fish to help understand variability in observed group sizes. Rather than calculating optimal group size, we modeled optimal choice and calculated the acceptable group sizes that arose from this choice. In the model, settling individuals weigh the fitness value of settling in a group against the expected fitness of searching another day and encountering other groups, choosing the option with the higher value. Model results showed that individuals settling on any given day in the settling season have several acceptable group sizes in which they can settle. The range of acceptable group sizes also changes across the season. Early in the season, when there is still adequate time to grow, large groups (with higher survival) have the highest fitness. Late in the season, when the ability to grow fast becomes more important, small groups, which convey fast growth rates (although riskier), have higher fitness. Thus, according to our model, even when fish all make the same, simple decisions, a variety of outcomes are possible, depending on the specific options encountered and temporally changing ecological pressures. Even when all fish behave optimally, initial variability in group sizes will persist.

The adaptiveness of grouping behavior and group size can be investigated using an optimality approach (Pulliam and Caraco, 1984). By contrasting the costs and benefits associated with grouping, individuals can choose whether to enter a group (Pulliam and Caraco, 1984) and what size group to enter (e.g., Baird and Dill, 1996). But the definition of an "optimal" group size (Caraco and Wolf, 1975; Giraldeau, 1988; Pulliam and Caraco, 1984; Ranta, 1993) can be problematical. Expectations of optimality are often based on unrealistic assumptions, such as perfect knowledge, no cost to sampling, or availability of all possible options. Because individuals will differ in their experiences (e.g., knowledge of environment or local availability of different options), it is important to model the decision process rather than the decision outcome. Thus, we believe it is important to separate the concept of an optimal "group size" from that of an optimal "choice" given constraints of individual experience (Sibly, 1983).

Coral reef fish provide an excellent opportunity to investigate optimality in choice of group size. Many species have a dispersive larval stage in the pelagic ocean waters and then return to the reefs where they settle into groups with conspecifics (Sale, 1980). For these fish, group size can affect an individual's growth rate and probability of survival (Booth, 1995; Forrester, 1990; Jones, 1987a,b). As group size increases, growth decreases (Booth, 1995; Forrester, 1990; Jones, 1987a); however, as group size increases, the probability of survival increases (Booth, 1995; Forrester, 1990; Jones, 1987b). Therefore, some coral reef fish are faced with a trade-off between growth and survival as a function of group size at the time of settlement (e.g., Booth, 1995; Forrester, 1990). Given a description of how these two rates change with group size, we can describe an "optimal" group size for settling larvae. However, in nature,

group-living coral reef fish of any given species occur over a range of group sizes under relatively similar environmental conditions (Shapiro, 1991). In this study, we sought to understand how differences among individuals and differences in their experiences might drive some of this variability in group sizes.

Here we look at how the trade-off between growth and survival can influence group size choice by settling larvae of the coral reef fish *Dascyllus albisella*. We specifically address three main aspects: (1) can variability in group-size choice arise under a specific set of unchanging conditions in a simple optimal decision model? (2) Is the range of acceptable group sizes influenced by the date of settlement? (3) Does body size at settlement affect the range of acceptable group sizes?

METHODS

To study group size selection by settling *D. albisella*, we developed a dynamic programming model. In this model, fish arrive at the reef and sequentially encounter groups in which they might settle. At each encounter, the newly arrived fish must decide whether to settle with that group or continue searching for a different group. A larva's decision is made by comparing the values of fitness that would accrue by settling in the currently encountered group to the potential fitness achieved by searching further. We defined fitness in this case as the product of size-specific fecundity of a female and the probability that it survives and grows to reach maturity by a specified time. Because larvae can settle over a protracted period of time during the year, we also asked how group size choice should vary throughout a single settlement season. We used data from the literature for *D. albisella* to set the timing of events and the values of parameters in the model.

Subject species

The larval stage for *Dascyllus albisella* lasts approximately 4 weeks (Wellington and Victor, 1989). After larval development in the pelagia, *D. albisella* return to the reef where they settle into branching corals (e.g., *Porites compressa* and *Montipora verrucosa*) as juvenile groups (Booth, 1992). When juveniles mature, they leave their groups and join the adult population in different areas of the reef (Booth, 1991). This allows for processes affecting juveniles and adults to be considered separately, without the effects due to interactions between life stages (Booth, 1995).

Dynamic programming model

We used dynamic programming techniques (after Mangel and Clark, 1988) to develop a model of group size choice. The model is a discrete time, sequential decision model, in which we represent the decision-making process of settling larvae of *D. albisella*. Upon arriving to the reef, a modeled larva encounters a potential settlement site containing i = 0-9 fish. A site with 0 fish is merely an unoccupied but otherwise acceptable coral head. Upon encountering a potential site, the larva can either settle or continue searching for another site. If the larva settles, the group becomes size $i + 1$.

An individual can arrive on any given day of the settling season. Arrival at the reef starts near the end of April and continues until mid-October (Booth, 1991). We assumed that spawning starts on April 1 and the planktonic phase lasts 26 days (Booth, 1991), such that arrival begins on April 26 and continues until October 15. We denote an individual's arrival date as t_0 (t_0 = 1, 2, . . . , 187), where 187 is the last possible day of arrival. We assumed in the model that fish arrive at

the reef with a limited energy reserve and feed only at low levels until they settled into a group. Considering expected starvation times for larvae of this size (Miller et al., 1988) and allowing for some low level of feeding, we assumed that larvae had six days to find and settle into a group. If, after six days of searching, the larva had not settled into a group, we assumed it had died. Note that this assumption does not imply that larvae actually search for six days (predation risk is high while searching), just that their energy reserves allow them to search no longer than six days. Thus, an individual's settling date was between t_0 and t_0 + 5. In the model, terminal time (T) was set as the number of days (T= 432) from the beginning of the settling season to the mid-point of the spawning season of the year after arrival.

The expected fitness of an individual that has arrived at the reef on day t_0 (t_0 = 1, 2, . . . , 187) and is searching over the reef at body size x on day t ($t = t_0, t_0$+l, . . ., t_0+ 5) and encounters a group of size i (i = 0, 1, . . . , 9) is $F_x(t_0,i,t)$, the maximum of the expected fitness from settling with that group, $V_{settle}(x,i,t)$, and the expected fitness from continuing to search another day, $V_{search}(x, t_0,i,t)$:

$$F_x(t_0, i, t) = \max_{settle,search} [V_{settle}(x, i, t); V_{search}(x, t_0, i, t)]$$

Expected fitness of settling

Expected fitness from settling on day t, given encounter with a group of size i, is equal to the probability that the larva survives from day t to T multiplied by its expected fecundity at terminal time:

$$V_{settle}(x, i, t) = \sigma_{i+1}^{T-t} R[X(x, i + 1, t)],$$

where σ_{i+1} is the daily probability of surviving in a group of size i+l (the encountered group size plus the newly settled individual), and $R[X(x,i+1,t)]$ is the fecundity of a fish of size $X(x,i+1,t)$, which is the size at time T of a fish that settled at size x into a group of size i on day t,

$$X(x, i + 1, t) = x + [g_{i+1}(T - t)],$$

where g_{i+1} is the group-size-specific growth rate (mm/day). We assumed that if an individual had not reached maturity by time T, then fecundity equaled zero. Thus, its fitness for settling would also be zero.

Expected fitness of searching

The expected fitness of continuing searching on day t given an encounter with a group of size i and arrival at the reef on day t_0 is the probability of surviving 1 more day of search multiplied by the probability of encountering a group of any given size on the next day, which is then multiplied by the expected fitness given that it makes the optimal decision (i.e., search or settle) upon encountering each potential group size:

$$V_{search}(x, t_0, i, t) = \begin{cases} 0 & \text{for } t \geq t_0 + 5 \\ \beta_x \sum_{j=0}^{9} \lambda_j F_x(t_0, j, t+1) & \text{for } t < t_0 + 5, \end{cases}$$

where β_x is the daily probability of surviving while searching, for a larva of size x, and λ_j is the probability of encountering a potential settlement site having a group of size j on the following day. If $t = t_0+5$, then $V_{search}(x, t_0, i, t) = 0$, so that $F_x(t_0, i, t_0+5) = V_{settle}(x,i,t)$.

Model parameters

Arrival size

Dascyllus albisella settles at body lengths of 10 to 16 mm TL (total length) (Booth, 1992). In our model, we varied larval size at arrival from 10 to 16 mm to assess body-size-dependent effects in group size choice. Because most larvae settle within a short time after arriving at the reef (Leis, 1991), we considered growth while searching as negligible; thus size at arrival was the same as size at settlement.

Growth rate and probability of survival after settling

Booth (1995) estimated mean juvenile growth rates of 0.16-0.30 mm/day and mean survival time (as persistence after settling) of 32-44 days. Daily growth and survival after settling are both functions of group size (Booth, 1995). We derived these parameters for our model indirectly from data reported in the literature. Using Booth's estimates for number of days (d_{i+1}) and proportion survival (s_{i+1}) to maturity of *D. albisella* as a function of group size, i+l (Booth, 1995), we calculated daily survival rates (σ_{i+1}) using the equation:

$$\sigma_{i+1} = (s_{i+1})^{1/d_{i+1}}.$$

Daily growth rates as a function of group size were determined by taking the difference between size at maturity (70 mm) and the median size at settling (13 mm) and dividing it by the number of days to reach maturity for each group size. The equations for daily growth and survival for the model were obtained by running least-squares regressions on our estimates (Table 1).

Probability of survival while searching

No field estimates of larval mortality are available (Leis, 1991). Mortality from predation is considered to be an important factor while larvae are in the pelagic zone (Leis, 1991). However, Johannes (1978) suggested that the pelagic stage of coral reef fish developed as a mechanism to escape high predation pressure in the reef environment. We have thus assumed that larvae returning to the reef will be subject to high predation risk before settling. Coral heads in the reef are used as refuges (Hixon and Beets, 1993), and so settling into the reef reduces predadon risk.

Because we found no estimates of larval mortality and had made the assumption that mortality while searching over the reef is higher than that for larvae that have settled, we also assumed that the daily survival rates for larvae when they reach the reef must be lower than their daily survival rates after they have settled as juveniles. Therefore, we set the probability of survival of the largest possible recruit (i.e., 16 mm) while searching equal to 95% of the *y*-

intercept value of the survival function for settled individuals. We then assumed the daily probability of survival while searching to be a declining function of size at the time of arrival (see Table 1).

Table 1
Parameter values and functions used in the model

Parameter	Function
Daily probability of surviving while searching	$\beta_x = 1.0 - a_1 \cdot e^{-(b_1 x)}$ $a_1 = 0.08$ $b_1 = 0.01$
Daily probability of surviving after settling into group of size $i + 1$	$\sigma_{i+1} = a_2 + b_2 \cdot (i + 1)$ $a_2 = 0.984$ $b_2 = 0.000508$
Growth rate (mm/d) in group of size $i + 1$	$g_{i+1} = a_3 - b_3 \cdot (i + 1)$ $a_3 = 0.274$ $b_3 = 0.00322$
Fecundity as a function of size, where $X(x, i + 1, t)$ is the size of a fish at time T that settled at length x on day t into a group of size i and $X(x, i + 1, t) = x + g_{i+1}(T - t)$	$R[X(x, i + 1, t)]$ $= \begin{cases} a_4 \cdot e^{b_4 X(x, i+1, t)} & \text{for } X(x, i + 1, t) \geq 70 \text{ mm} \\ 0 & \text{for } X(x, i + 1, t) < 70 \text{ mm} \end{cases}$ $a_4 = 30.5$ $b_4 = 0.058$

Group size is indicated by $i + 1$ (i.e., encountered group size i plus the newly settled individual) and length (mm) at time t is indicated by x.

Group-size distribution

Group sizes in *Dascyllus albisella* can range from 1 to 15 individuals, and mean group size ranges from 3.3 to 7.5 individuals (Booth, 1995). However, no estimates of group-size frequency distributions for *D. albisella* are available. Booth (1992) reported only 30% occupancy of coral heads within one reef. Thus, we assumed a negative binomial probability distribution of encountered group sizes to reflect the high probability of encountering an empty coral head (i = 0). We used a mean encountered group size of five. Probabilities were normalized such that

$$\sum_{i=0}^{9} \lambda_i = 1.$$

Maturation size and fecundity

Dascyllus albisella are considered juveniles when 15-70 mm TL. Sexual maturity is attained at around 65-70 mm TL (Booth, 1991), and maximum adult size is approximately 140 mm (Stevenson, 1963). We modeled size at maturity as 70 mm.

Size-specific fecundity was estimated from data on length and number of eggs reported by Stevenson (1963). Stevenson (1963) measured fecundity values ranging from 12,700 to 43,700 eggs/female; however, sample size was low (n = 9 females) and the size range of the females limited (104-125 mm). We used an exponential function that approximated the fecundity

values reported by Stevenson (Table 1).

Sensitivity analysis

The trade-off between growth and survival likely is driving many of the model results. Therefore, we need to know if inaccuracies in our estimates of the growth and survival parameters could lead to different model responses. We also recognize the possibility that interactions among parameters might be important. For instance, if we change growth rates, it not only might affect the growth-survival trade-off, but also might interact with the effect of size-specific fecundity. In addition, our estimate of the length-fecundity relationship for *D. albisella* is limited by a low sample size and narrow range of lengths; thus we assessed the influence of the shape of the length-fecundity relationship on the model's performance.

We looked at model sensitivity using Yates' algorithm, a 2^k factorial design of changes in parameters (Box et al., 1978). For this analysis, we changed five parameters: the slope and *y*-intercept values of both the group-size-dependent growth and survival functions, and the shape of the length-fecundity relationship (see Table 1). New estimates of the parameters for growth and survival functions were obtained by decreasing and increasing the original values by 10%. A new length-fecundity relationship function was established by fitting Stevenson's (1963) fecundity data to a linear function. In the analysis, a factor or a combination of factors was considered to have a significant effect on model response if the proportional change between a baseline observation and the change in the value of the response attributed to the factor(s) was greater than the proportional change of the original parameter(s) value(s) for growth and survival (i.e., 20%). For the length-fecundity relationship, we considered a 10% minimum change to be a significant effect.

Because of the uncertainty of our original parameter values, we were interested in the qualitative patterns of group size choice as a test of the conceptual framework of our model more than in the precise fitness values. We looked at two responses: the "last day" for which only one group was acceptable for settling and the range of acceptable group sizes on day 75 of the model run. Day 75 was arbitrarily chosen because it is close to the middle of the range of days for which a larva can settle and still reach maturity by terminal time.

RESULTS

On any given day during the settling season, for an individual of a given length (13 mm) just arriving to the reef, a range of group sizes is acceptable (Figure 1). This means that when an individual encounters a group in this range of sizes, it should choose to remain there rather than continue searching, even if a better group might be encountered the following day. The sudden discontinuity in value of settling at, for example, group size = 7 on day 119, is an artifact of using a single terminal time in the model. A more probabilistic approach to assigning terminal times would result in a less discrete step in fitness values (see Discussion).

Effect of time of settlement on group size choice

Early in the settling period, *D. albisella* individuals just arriving to the reef would do better settling into the first group of conspecifics encountered (except a group of 0) rather than searching for a group with a higher fitness value (Figure 1a). Later during the settling period, the fitness of settling into large groups drops below the value of continuing searching. When individuals encounter these groups, they maximize fitness by searching another day for a smaller group rather than settling (Figure lb). As the settling season progresses, the range of acceptable

groups continues to narrow by shifting further toward small groups (Figure 1c).

Effect of size at settlement on group size choice

Fitness from settling into a given group size on a given day is greater for large than for small individuals (compare bars between Figure 2a,b). Fitness for continuing to search on a given day is also greater for larger than small individuals (compare lines between Figure 2a,b), such that qualitative patterns in ranges of acceptable group sizes are similar for large and small individuals (Figure 2). However, later in the settling season, the range of acceptable group sizes narrowed earlier for small than for large individuals (Figure 2c,d).

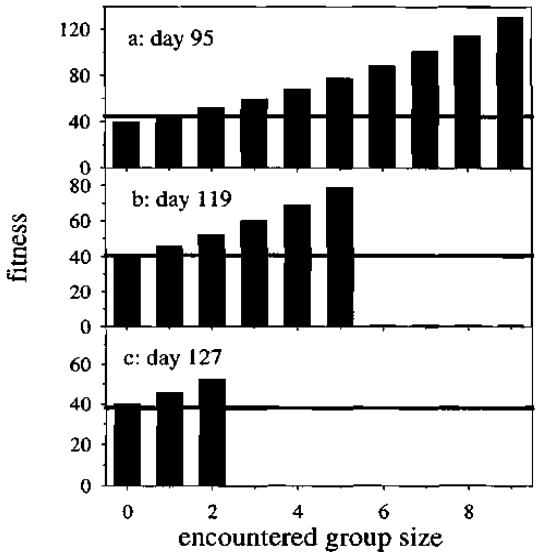

Figure 1
Expected fitness for a 13-mm individual encountering a group of a given size on the first day after arrival at the reef. Bars indicate expected fitness of settling into the encountered groups; horizontal lines represent the expected fitness of continuing searching for a better group. Modeled fish chose the maximum of searching and settling at each encounter. Results are shown for individuals arriving to the reef on (a) day 95, (b) day 119, and (c) day 127.

Effect of reef residence time on settlement choice

The longer an individual has been searching on the reef, the less value there is in continuing searching. Because there is a 6-day energetic limit to the number of days a fish can search, by the fifth day on the reef, searching becomes a risky choice. The number of days an individual has been searching on the reef does not affect the expected fitness from settling into a group of a particular size, so more group sizes may become acceptable as the larva spends more days searching.

Parameter sensitivity

Overall, qualitative patterns in time dependence and body size dependence of ranges of acceptable group sizes were robust to changes in parameter values and functions. Output from runs of the model using modified parameter values for group-specific growth rate, group-specific probability of survival, and fecundity showed the same qualitative patterns of group size choice by *D. albisella* as runs with the original parameters. An increase in growth rate extended the number of days in the settling season during which a fish could settle and still reach maturity by

terminal time in the model (Table 2). Decreasing the growth rate reduced the number of days a fish could settle and still reach maturity. Changes in growth rate and fecundity had effects on the range of acceptable group sizes for day 75 of the settling season. A decrease in growth rate, as well as switching the length-fecundity relationship from an exponential to a linear relationship, had the effect of narrowing the range of acceptable group sizes by making the larger groups unacceptable (Table 2). An increase in growth rate had no effect on the range of group sizes. Changes in the probability of survival had no effect in either of the target responses.

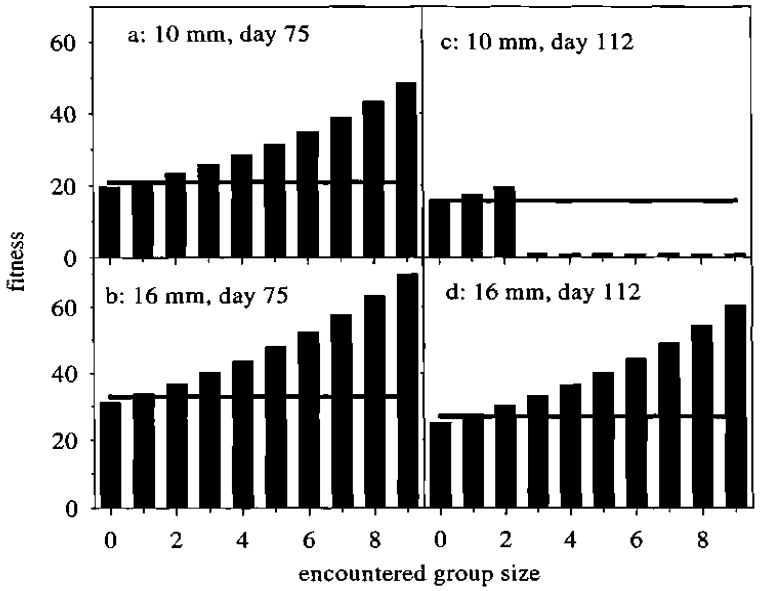

Figure 2
Expected fitness for (a,c) 10-mm and (b,d) 16-mm individuals encountering a group of a given size on the first day of arrival at the reef on day 75 and day 112. Bars indicate expected fitness of settling into the encountered groups; horizontal lines represent the expected fitness of continuing searching for a better group. Modeled fish chose the maximum of searching and settling at each encounter.

Table 2
Parameters found to have significant effects on the two target responses of the sensitivity analysis

Target response	Parameter change	Effect on response
Last day to settle and still reach maturity by terminal time in model	Increase growth rate	Last day shifts to later in season
	Decrease growth rate	Last day shifts to earlier in season
Range of acceptable group sizes on day 75 of settling season	Decrease growth rate	Decrease in size of largest acceptable group size
	Linear length-fecundity relationship	Decrease in size of largest acceptable group size

A parameter is considered to have a significant effect if the difference between the baseline observation and the change in the value of the response attributed to that parameter is greater than the proportional change in the value of the parameter.

DISCUSSION

Organisms that live in groups often face a trade-off between the associated costs and

benefits (Booth, 1995; Pulliam and Caraco, 1984). Living in a large group can increase survival through better predator detection (Caraco, 1979; Lima, 1995; Rasa, 1989) or a dilution effect (Dehn, 1990; Foster and Treherne, 1981; Roberts, 1995; Wrona and Dixon, 1991). However, it can also lower feeding rate due to competition for food between members of the group (Clifton, 1990; Coates, 1980; Forrester, 1991; Jones, 1987a; Rasa, 1997). Although we could calculate an "optimal group size" from measured relationships between growth and survival (e.g., Booth, 1995), we chose to model optimal "choice" instead. All individuals modeled used the same optimal choice rules, yet faced differences in individual experience (i.e., differences between individuals in the actual group size encountered on a given day). Model results indicate how variation in the optimal group size chosen could arise on a single day from otherwise identical individuals and thus how initial variation in group sizes can persist.

Our model of group size choice for *Dascyllus albisella* showed that early in the settling season, settling into large groups provided a higher fitness than settling into small groups. Despite slow growth in the large groups, the high probability of survival coupled with adequate time to grow before their first spawning season made large groups more valuable. Early in the season, a group size of 10 individuals is the optimal group size (e.g., Figure la). However, early in the settlement season, when faced with the decision of continuing searching or settling into the most recently encountered group, settling is always a better choice (regardless of the group size and its availability) than the survival uncertainties and growth delay from searching for another group. As the settling season progresses, the value of large groups declines because fast growth becomes more important than an increase in survival probability. So later in the season, when faced with a decision of settling into a large group or continuing searching, individuals should continue searching to find smaller groups (Figure 1b,c).

The results discussed above are in part driven by specific quantitative assumptions in the model, and thus it is important to discuss their qualitative generality in the face of changed assumptions. If a fish cannot grow to maturity in a particular group by the middle of the next spawning season, we set its fitness to zero in that group. In reality, a fish will have future spawning times available, so that fitness should not actually drop to zero. But expected fitness would indeed be greatly reduced, and the emphasis late in the season should still be on maximizing growth. Thus, our qualitative results of bias toward small groups late in the season should still stand under relaxation of the "zero fitness" assumption.

Although our results are specific to *Dascyllus albisella* because we used parameter values derived from studies of this species, general patterns in results will be similar for the many coral reef fish species having planktonic larvae that settle into groups as juveniles on the reef. The most useful generality from this study, however, is in the approach of modeling the decision rather than the outcome. Previous investigators have demonstrated this, primarily in investigations into why "stable" group sizes tend to be larger than "optimal" group sizes (Clark and Mangel, 1984; Giraldeau, 1988; Sibly, 1983). In those studies, it was noted that group size is determined by decisions of individuals external to the group. As long as joining the group is better than being solitary, the group will increase, regardless of the optimal group size. Whereas those studies were focused on explaining how differences between a single stable and an optimal group size could arise, ours was focused on explaining how multiple acceptable group sizes rather than a single optimal size could arise, though both problems emphasized similar mechanisms. In our study, we were interested specifically in how individual experience (e.g., random encounters with groups) and conditions (e.g., body size and time of arrival to reef) produce variability in group sizes chosen, again, through decisions made by individuals not yet

in a group.

Summary

In this study, we developed a dynamic programming model of an optimal decision process of group size choice that considers the trade-off between growth and survival as a function of group size in the coral reef fish *Dascyllus albisella*. Despite only moderate confidence in quantitative estimates of some parameters, the qualitative patterns that arose from the model proved to be robust in a sensitivity analysis of the model. According to our model, when fish make optimal decisions, the result is a variety of possible outcomes that depend on the specific choices encountered and temporally changing ecological pressures; even when all fish behave optimally, we should see variance in group sizes chosen.

We thank D. J. Booth for his comments and suggestions regarding our interpretation of his data during the development of our model. Suggestions from R. Ydenberg and two anonymous reviewers greatly improved the manuscript. This study represents a portion of the dissertation work of F.A.M. The work was funded in part by a Graduate Teaching Associateship from The Ohio State University to F.A.M., a National Science Foundation grant (DEB 9410327) to E.A.M., and a National Oceanic and Atmospheric Administration grant (NA86RG0053) to E.A.M.

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